2-20-2014

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Journal of Applied Ichthyology

J. Appl. Ichthyol. 30 (2014), 1428–1440
Published 2014. This article is a U.S. Government work and is in the public domain in the USA
ISSN 0175–8659

Received: February 20, 2014
Accepted: August 18, 2014
doi: 10.1111/jai.12607

Survival of hatchery Gulf sturgeon (*Acipenser oxyrinchus desotoi* Mitchill, 1815) in the Suwannee River, Florida: A 19-year evaluation

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Summary

An experimental release of 1192 hatchery-reared, individually PIT tagged, 220 days old (296–337 mm TL) Gulf sturgeon, *Acipenser oxyrinchus desotoi*, was undertaken in 1992 in the Suwannee River, Florida. The original objectives of the 1992 release experiment were to: (1) evaluate survival rate of cultured Gulf sturgeon in the wild vs survival rate of their wild 1992 cohort counterparts, (2) determine the differential effect of release site within the river upon long-term survival, and (3) evaluate comparative growth rates of recaptured hatchery vs captured wild 1992 cohort Gulf sturgeon. The present investigation addressed those original objectives, plus an additional fourth objective: (4) evaluation of hatchery fish recapture rate change over the 19-year experiment. The primary objective was to determine efficacy of potential conservation aquaculture for this species in terms of long-term survival in the wild. Follow-up 1993–2011 gill net sampling in freshwater reaches (rkm 4–237) and the estuarine river mouth (rkm −6 to 4) yielded recaptures representing 13.0% of the total released. Mean annual hatchery fish mortality (including emigration) rate estimated for the 19-year period (1993–2011) was more than twice that for same cohort wild fish. Mark-recapture survival probability (phi) for hatchery fish, 1993–2011, was substantially lower (0.733) than for their wild counterparts (0.888). Mean annual hatchery fish recapture rate, as a percentage of all 1992 cohort fish recaptures, declined significantly after age-7, coinciding with age of onset of migration into the open Gulf of Mexico. Hypothesized causal factors may be differentially lower fitness in the marine habitat or permanent outmigration due to natal river imprinting failure. Hatchery fish recapture rates varied significantly for fish from the ten release sites, being highest near the river mouth, and lowest for the furthest upriver sites in the Suwannee River and its Santa Fe River tributary. Hatchery fish also displayed a significantly lower growth rate than their wild counterparts through age 3000 days. Cumulative hatchery fish mortality of 99.87% over 19 years predicts <3 individuals would have survived through 2011. From the results of the 1992 release experiment, hatchery supplementation as a Gulf sturgeon conservation measure does not appear to be an effective option.

Introduction

The most fundamental question to address regarding a program of artificial population supplementation to promote restoration and conservation of an imperiled fish species is the ultimate efficacy of that program. That is, what number and proportion of released fish will ultimately survive and remain in the natal river to sexual maturity. The number of fish reared and released may be immaterial, if the ultimate number of fish surviving to sexual maturity is small due to apparent mortality (i.e. real mortality plus emigration). This is particularly true for a late-maturing species in which cumulative mortality from the fingerling release stage to adulthood exacts a substantial toll before sexual maturity can be achieved. The present investigation quantifies the long-term (through 19 years) survival of 1192 Gulf sturgeon, *Acipenser oxyrinchus desotoi*, reared in the laboratory from wild Suwannee River parents, PIT-tagged, released into the Suwannee River in November-December 1992, and monitored by net sampling through April 2011. The hatchery fish experiment was an early measure aimed at developing conservation aquaculture for the Gulf sturgeon, in accordance with restoration options advanced in the Endangered Species Act (ESA) recovery plan for this threatened species (USFWS, GSMFC, NMFS 1995).

A second fundamental question is which release sites will potentially yield the greatest survival rate. Consequently, in the 1992 experiment, survival by release site was considered a critical metric to inform any subsequent program of Suwannee River Gulf sturgeon stocking. Results of early telemetry studies had earlier suggested that Suwannee population Gulf sturgeon not only homed to their natal river, but also to particular natal sites or ‘home areas’ within the river (Clugston et al., 1995; Carr et al., 1996). It was hypothesized that survival of stocked fingerlings might thus be differentially influenced by release site due to variations in site-specific habitat quality.

In anticipation of ESA 1991 listing of the Gulf sturgeon, the U.S. Fish and Wildlife Service (USFWS) embarked upon a program of experimental culture of the species beginning in 1989. Undertaken in cooperation with the former Caribbean Conservation Corporation (CCC) (now The Sea Turtle Conservancy) and the University of Florida (UF), experimental culture was aimed at development of the technology to enable large-scale rearing, should supplementation of wild Gulf sturgeon populations be deemed necessary. It was also aimed at providing hatchery fish to enable laboratory investigation of life history requirements (e.g. Foster et al., 1995; Altinok et al., 1998; Bardi et al., 1998; Kynard and Parker, 2004). In 1989, USFWS undertook streamside artificial spawning of Suwannee River Gulf sturgeon (Parauka et al., 1991). Subsequently, culture operations were moved to the USFWS National Fisheries Research Center (NFRC) laboratory (now the U.S. Geological Survey [USGS] Southeast Ecological Science Center) in Gainesville, FL. Artificial spawning of wild caught Suwannee River Gulf sturgeon was attempted in 11 years, 1989–1999, succeeding (i.e. viable fry being produced) in six of those years. An unexpectedly successful spawning (gametes of one female and three males) was achieved in April 1992, resulting in several thousand fry, substantially exceeding laboratory research needs. As an alternative to euthanasia, a decision was made to grow out the fry to age 220 days for release into the Suwannee River to evaluate survival in the wild.

The original objectives of the 1992 release experiment were to: (i) evaluate survival rate of cultured Gulf sturgeon in the wild vs survival rate of their wild 1992 cohort counterparts, (ii) determine the differential effect of release site within the river upon long-term survival, and (iii) evaluate comparative growth rates of recaptured hatchery vs captured wild 1992 cohort Gulf sturgeon. The present investigation addresses those original objectives, and an additional fourth objective: (iv) evaluation of hatchery fish recapture rate change over the 19-year experiment.

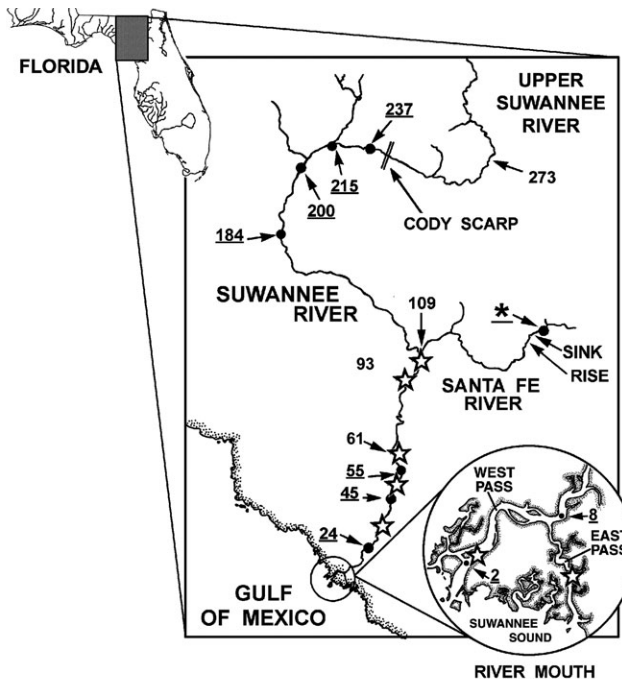

Fig. 1. Suwannee River, Florida, indicating 1992 release sites (underlined rkms or asterisk) for hatchery-reared Gulf sturgeon. Asterisk = Santa Fe River release site. Stars next to rkm: Primary gill-net recapture sites. Circle inset details East Pass and West Pass, both major post-release sampling areas

Materials and methods

Study area

The early life history of wild Suwannee River Gulf sturgeon begins on localized gravel bed spawning grounds 202–221 river kilometers (rkm) from the river mouth (Fig. 1) (Sulak and Clugston, 1998, 1999). Developmental habitat for age-0 Gulf sturgeon includes freshwater river reaches primarily below rkm 221, although age-0 juveniles have been captured (Sulak and Clugston, 1998) and reported (USGS, unpubl. data) upstream of the spawning grounds. Larvae and early juveniles disperse variable distances downstream (Sulak and Clugston, 1998; Kynard and Parker, 2004), but do not descend to the saline river mouth. Potential downstream habitat also includes the Santa Fe River (Huff, 1975; Flowers and Pine, 2008), the only major tributary joining the Suwannee River along its middle reaches. This tributary extends for about 113 rkm upstream from the confluence with the Suwannee River at rkm 109 (Fig. 1). However, except under conditions of very high water, from O'Leno Sink it flows underground (5 km by land), through a continuous karst cave system, re-emerging at the Santa Fe Rise, 41 rkm from the Suwannee confluence (155 rkm from mouth of Suwannee River). Such exceptionally high water conditions were not observed from November-December 1992 (release) through April 1993 (USGS gage 02320500: http://waterdata.usgs.gov/nwis/rt).

Marking and release

Hatchery Gulf sturgeon had attained the minimum 200 mm TL threshold for PIT tagging by September-October 1992. Individually numbered tags were injected sub-dermally at the base of the dorsal fin. PIT tag retention (Clugston, 1996) was verified immediately prior to release, 2–3 months after tag application. Replacements were injected, as needed. Six to seven days before release, a sample of about 10% of 800 fish prepared for release by USFWS were weighed and measured in the laboratory to determine mean TL and weight. The remaining fish for release by UF were individually weighed and measured prior to release.

Nine stocking sites at rkm 2, 8, 24, 45, 55, 184, 200, 215, and 237 in the Suwannee River mainstem, and another at Santa Fe River, rkm 46 in this tributary (equivalent to rkm 155 in the overall Suwannee River system), were chosen to span the hypothesized range of age-0 Gulf sturgeon nursery habitat in the Suwannee River drainage (Fig. 1, Table 1). For the USFWS releases only (not for UF releases), river water was gradually mixed into hatchery truck water (20°C) for about 45 min prior to stocking to acclimatize fingerlings to ambient river temperatures (10.7–14.7°C). Fingerlings (N = 1192) were released at age ~220 days. Two groups, age 220 days (using the hatching day of 16 April 1992 as day-1), were released by UF on 22 November 1992: 197 were released at the Santa Fe River site (mean TL 294 mm, mean wt 88 g); 198 were released in West Pass (Fig. 1, inset) Suwannee River rkm 2 (mean TL 296 mm, mean wt 84 g). Eight groups, each of 98–100 fingerlings, age 243–244 days (mean TL 337 mm, mean wt 135 g) were released by USFWS at eight Suwannee River sites between rkm 8–237 on 15 and 16 December (Fig. 1, Table 1).

Table 1
Recapture rates by release site (rkm) for hatchery Gulf sturgeon with χ^2 variance-to-mean ratio test applied across sites, and comparative captures by rkm range for 1992 cohort wild Gulf sturgeons. Overall recapture rate (21.07%) used as the 'expected' rate for the χ^2 variance-to-mean ratio model test

1992 released hatchery-reared Gulf sturgeons					1992 cohort wild Gulf sturgeons			
Release site (rkm)	Released N_i	Total recaptures N_r	Totalrecaptures % overall total	Observed recaptures per 100	Expected recaptures per 100	Capture site range (rkm)	Captures & recaptures N_r	Captures & recaptures % total
2	99	52	23.96	52.53	21.07	−6[b] to 3.5	222	67.5
8	100	31	14.29	31.00	21.07	34–38	10	3.0
24	100	16	7.37	16.00	21.07	40–49	10	3.0
45	99	24	11.06	24.24	21.07	55–61	35	10.6
55	100	18	8.29	18.00	21.07	71–94	11	3.3
155[a]	197	12	5.53	6.09	21.07	108–120	9	2.7
184	101	17	7.83	16.83	21.07	139–190	9	2.7
200	98	24	11.06	24.49	21.07	200–205	7	2.1
215	100	20	9.22	20.00	21.07	214–221	14	4.3
237	198	3	1.38	1.52	21.07	237	2	0.6
Total	1192	217	100.00	210.70	210.70		329	100.0
Overall recapture rate, all years			21.07					
				χ^2	84.05			
				Df	9			
				Upper critical	16.92			
				P	<0.001			

[a]Santa Fe River rkm 46 release site, [b]Negative rkm = Suwannee estuary.

Recovery techniques

The sampling design was not random and overall methods used were not amenable to expression of data in terms of catch per unit effort. Marking with tags (using both PIT in dorsal fin base and T-bar spaghetti tags in pectoral fins) and recapture of wild Gulf sturgeon in the Suwannee River by anchored gill net had previously been initiated by USFWS beginning in 1988 (Clugston et al., 1995), continuing through 1992. In 1993 (January through December, 5–12 days per month) and 1994 (January through November, 2–9 days per month), the USFWS used the same methods to sample and tag both wild and hatchery sturgeon. Primary sampling sites in the Suwannee River were rkms 0, 1.0, 2.5, 3.0, 34.0, 36.0–38.0, 40.0–40.5, 55.5, 71.0, 73.2, 93.2, 109.0–109.5, 189.0–190.0, 200.0–200.2, 221.0 and 237.0 (USGS unpubl. data). Sampling sites lying between rkms 34.0 and 200.2 were known areas (Fig. 1) of spring to fall congregation and holding (Clugston et al., 1995). Additional sites upstream of rkm 237.0 (to rkm 286.0) were also infrequently sampled. Sampling gear consisted of anchored single-mesh monofilament gill nets (primarily 6.5–9.0 cm bar mesh [measured point to point]) and 'experimental' multi-mesh nets, each comprised of four 7.6 m long panels (primarily 2.5, 2.8, 5.1 and 6.4 cm bar mesh) (Clugston et al., 1995). Four to 6 nets, varying from 15–61 m length, 1.5–2.4 m depth, were set at each sampling site for 4–12 h, and checked repeatedly, approximately every hour. In the context of the hatchery release experiment, 1993–1994 sampling effort was focused on the mouth of West Pass, rkm 0–2.5 (Fig. 1, inset) where juvenile Gulf sturgeon, including hatchery fish, were expected to congregate for feeding in winter based on prior USFWS sampling d ta. In 1993, sampling was conducted on 58 days at West Pass and 88 days at 12 other primary sampling sites (rkm 33–237). In 1994, 44 days were spent at West Pass and 23 days at six other sampling sites (rkm 40–200).

In 1993, the USFWS NFRC was transferred to the National Biological Survey, itself subsequently incorporated into the USGS in 1995. The Gulf sturgeon research program continued under USGS with sampling methods in 1995–1997 shifted to prioritize gill net capture of subadults (>1000 mm TL) and adults (>1350 mm TL ♂♂, >1500 mm TL ♀♀) during the fall emigration (October-November) to enable population structure analysis (Sulak and Clugston, 1999). Gill net mesh sizes were too large (10.2–12.7 cm bar measure, in nets 305 m long, 3.7 m deep) to effectively capture most age-2 through age-4 hatchery juveniles (ca 350–900 mm TL) (Sulak and Clugston, 1999; Sulak and Randall, 2002). Sampling in 1998–2011 was accomplished primarily with 10.2 cm bar mesh drift nets (100 m long, 4 m deep) deployed over spring-fall holding areas (Fig. 1), targeting both wild and hatchery Gulf sturgeon. A small number of samples were obtained with 5.1 cm and 12.7 cm bar mesh drift nets. Sampling in 2011 was accomplished with 10.2 cm bar mesh set nets (61 m long, 2.0 m deep). By 1998, hatchery Gulf sturgeon were large enough (>1000 mm TL) to be vulnerable (Table 2) to the primary 10.2 cm bar mesh drift nets employed. Beginning in 1998, all nets were tended continuously, and fish removed immediately, to minimize net mortalities (three mortalities occurred in 1998; zero mortalities from 1999 to 2011). All USFWS and USGS recaptures were weighed, measured, examined and scanned for previously-applied tags, and tagged if previously unmarked. Upon first recapture, hatchery Gulf sturgeon were also tagged with colored, individually numbered T-bar tags inserted in both pectoral fins. These served for rapid visual identification of recaptured fish, and maximized re-identification potential, i.e. PIT plus T-bar.

Table 2
Comparative recapture data by sampling year for hatchery Gulf sturgeons, with χ^2 variance-to-mean ratio test across years. Overall recapture rate among all years (12.18%) used as the 'expected' recapture rate for the χ^2 variance-to-mean ratio model test. Bold = estimated minimum or maximum TL for hatchery fish based on estimated TL-at-age for wild Gulf sturgeons from pectoral fin spine ring-count aging (Sulak and Randall, 2002; Berg et al., 2007; Randall and Sulak, 2007)

Year	Hatchery fish age (year)	Observed total hatchery fish recaptures (N_h)	Observed first hatchery fish recaptures (N_1)	Hatchery fish TL range (mm)	TL interval applied (mm)	Total wild fish captures[a] (N_w)	Hatchery fish as % total ($N_h + N_w$)	Expected hatchery fish recaptures	Captures of 1992 cohort wild fish (N_c)
1993	1	69	63	351–647	350–650	359	16.12	52	259
1994	2	46	35	528–703	525–705	313	12.81	43	17
1995	3	5	3	673–794	670–795	29	14.71	4	3
1996	4	6	3	830–910	830–910	17	26.09	3	7
1997	5	8	6	926–1026	925–1030	25	24.24	4	10
1998	6	39	21	930–1212	930–1215	227	14.66	32	11
1999	7	30	15	1000–1266	1000–1270	138	17.86	20	9
2000	8	5	4	1124–1372	1120–1375	34	12.82	5	3
2001	9	2	1	1210–1230	1210–**1450**	72	2.70	9	0
2002	10	2	1	1256–1314	1255–**1510**	68	2.86	8	3
2003	11	0	0			0			1
2004	12	0	0			0			
2005	13	1	0	NA	**1350–1650**	20	4.76	3	0
2006	14	3	3	1524–1694	1520–1695	98	2.97	12	4
2007	15	1	0	1376	1375–**1695**	130	0.76	16	1
2008	16	0	0		**1375–1750**	15	0.00	2	0
2009	17	0	0			0			
2010	18	0	0		**1375–1900**	19	0.00	2	0
2011	19	0	0		**1375–2000**	20	0.00	2	1
Subtotals 'N'		217	155			1564			329
Total 'N' ($N_h + N_w$)						1801			
Overall recapture rate, all years $[N_h/(N_h + N_w)]^a 100$				12.05%					
Unweighted mean recapture rate, all years				9.59%			χ^2	57.64	
Mean recapture rate (1993–2000)				17.41%	5.08%		df	15	
Mean recapture rate (2001–2010)				1.76%	1.81%		Upper crit.	25	
							P	<0.001	

[a]Total wild fish captured in a given sampling year – within the probable minimum and maximum TL limits (refer to Fig. 2) for a 1992 wild cohort Gulf sturgeon.

Each fish was weighed (nearest 1.0 g for individuals <100 g, nearest 10 g for larger individuals <1000 g weight, nearest 100 g for larger individuals <10 000 g, and nearest 1000 g for fish >10 000 g). Gills were irrigated during processing. Each Gulf sturgeon was released immediately upon processing, typically within 2–3 min of removal from the net.

Additional recaptures were accomplished by UF during spring 1997–2001 sampling (variable periods: February through April) in anchored gill nets (2–10 nets, 30–46 m long, 3.0–3.7 m deep, 12.7 cm bar mesh) set between rkm 2–4 in East Pass (Fig. 1). This sampling targeted adult Gulf sturgeon (Clugston et al., 1995; Carr et al., 1996) to assess reproductive stage of captured individuals. Wild Gulf sturgeon collected by CCC and UF prior to 1996 were tagged with Monel tags (metal cattle ear tags); after 1996, wild Gulf sturgeon were tagged with T-bar tags (one in each pectoral fin) and PIT tags (inserted sub-dermally into the flesh at base of dorsal fin). Hatchery Gulf sturgeon were also tagged with T-bar tags upon first recapture, or with replacement T-bar tags upon subsequent recapture, as needed.

Hypotheses and statistical tests

The first null hypothesis tested (H1) was that hatchery Gulf sturgeon survival and apparent mortality (actual mortality plus emigration) did not differ from same cohort (1992-spawned) wild Suwannee River Gulf sturgeon survival and apparent mortality. The second null hypothesis (H2) was that hatchery Gulf sturgeon recapture rate did not differ among the ten release sites (vs overall hatchery fish recapture rate for all sites, all years combined). The third null hypothesis (H3) was that hatchery fish growth rates (TL-at-age, weight-at-age) did not differ from those of their wild 1992 cohort counterparts. The fourth null hypothesis (H4) was that annual hatchery fish recapture rate did not differ among the 13 sampling years yielding hatchery fish recaptures (vs overall hatchery fish recapture rate, all 16 sampling years combined) within the 19-year follow-up period. Hatchery Gulf sturgeon recapture rate for a given year was calculated as total hatchery fish recaptures for that year divided by total hatchery fish recaptures plus same-size range wild fish captures for the same year (Table 2). When three or more hatchery fish were recaptured, their TL range was used to bracket same-size wild fish captures to enumerate. When <3 hatchery fish were recaptured, the TL used to bracket wild fish captures was estimated from Suwannee River Gulf sturgeon TL-at-age data (Pine et al., 2001; Sulak and Randall, 2002; Randall and Sulak, 2007; USGS, unpubl. data).

Upon *a posteriori* inspection of release site recapture rate data, a t-test was undertaken to compare mean recapture rates for the 8-year period 1993–2000 (comprising eight sampling years) vs those for the 11-year period 2001–2011 (comprising eight sampling years). Years with no sampling conducted were excluded from mean rate calculations.

Test of H1 was performed using Cormac-Jolly-Seber (CJS) models in Program MARK (White and Burnham, 1999), with the wild fish population consisting of the appropriately-sized wild Suwannee River individuals captured and tagged in 1993. Tests of null hypotheses H2 and H4 were performed using a χ^2 variance-to-mean model ($P = 0.05$). Additionally, upon a posteriori inspection of recapture rate data, a t-test was undertaken to compare mean recapture rates for the 8-year period 1993–2000 (comprising eight sampling years) vs those for the 11-year period 2001-2011 (comprising eight sampling years). Years with no sampling conducted were excluded from mean rate calculations. Hypothesis H3 was evaluated by ANCOVA upon linear regressions (Zar, 1994) to test for significantly different TL-at-age and weight-at-age growth rates (individuals <3000 days old) for 1992 hatchery fish vs 1992 cohort wild fish.

Program MARK survivability, capture probabilities, apparent mortality estimates, and population estimate

Hatchery and wild (1992 spawn year) fish survival (phi) and recapture probabilities (p) were generated in Program MARK (White and Burnham, 1999) using the recaptures only mode (CJS model), with the recapture histories referenced to year-of-capture only. Wild 1992-spawned fish were extracted from the overall capture history file by selecting all wild fish caught in 1993 with TLs between 300 and 600 mm (the larger size fish were all caught in late 1993). Total 1993 'n' for the wild fish comparison was 224 (Table 3). This methodology will not yield accurate wild population estimates for the 1992 wild cohort since only fish that were captured in 1993 were included in the model population (i.e. a fish that was captured for the first time in 1994, and based on size belongs to the 1992-spawned wild cohort, was not included in the model population). Restriction to 1993-captured wild Gulf sturgeon provides for the most parsimonious model for survival probability. Within-year recaptures were collapsed to a single event. Several models were run, with the best-supported being the fixed survival, time-dependent recapture [phi(.) p(t)] model. Population estimates were generated using the time-dependent recapture probabilities and the number of recaptures for that year. Estimates for 2003, 2004, and 2009, years with no effort, were censored to zero. CJS models cannot distinguish between true mortality (fish death) and emigration (permanent departure from the river population). Either results in an individual being unavailable for sampling. Thus, apparent mortality (fish death + emigration) was calculated as the inverse of survival probability.

Growth rate analyses

While comparative survival rate is the primary measure of the success of hatchery vs wild Gulf sturgeon used in this study a secondary success metric is comparative growth rate. The same hatchery fish hatching date of 16 April 1992 was also assigned as day-1 for all wild fish identified as having been spawned in spring 1992 (thus identified by TL correspondence upon capture in 1993 and by tag correspondence thereafter). To compare hatchery fish vs wild fish growth rates, linear regression plots of TL-at-age (days) and cube root transformed weight-at-age (days) were prepared, with resultant data analyzed via ANCOVA (Zar, 1994; F test, $P < 0.05$) using GraphPad Prism 6® software (GraphPad Software, Inc., La Jolla, CA).

Table 3
Program MARK Phi(.)p(t) model determined survival values (phi) for Gulf sturgeon

Study group	Total N	Recaps (N_r)	Phi	Mortality rate, % (95% CI)
Hatchery fish 1992	1192	217 of 155 unique fish	0.7334512	26.66 (22.1–31.8%)
Wild fish 1993 (300-599 mm TL)	224	70 of 54 unique fish	0.887672	11.22 (4.2–26.8%)
Wild fish – all 1986–2013	5972	3061 of 1343 unique fish	0.8826157	11.74 (10.8–12.8)

Results

Wild fish captures from the 1992-spawned cohort

A TL-at-age relationship for Suwannee River wild Gulf sturgeon had previously been established from pectoral fin spine ring-count aging (Sulak and Randall, 2002). By total length correspondence, juveniles <600 mm captured throughout 1993 were considered to have been spawned in 1992. Including first captures and recaptures of these same individuals, 1993 through 2011, comparative data were available for 329 captures of 224 wild Gulf sturgeon (Table 3) from the spring 1992 spawned cohort (Tables 1, 2). Between 1994 and 2011, 54 of these same individuals were recaptured 70 times (Table 2). The last recapture from the 1992 wild cohort occurred in 2011.

Hatchery fish recaptures from the 1992 release

Samplings for hatchery-reared Gulf sturgeon from the experimental release in November-December 1992 were conducted between January 1993 and April 2011 (last hatchery fish capture recorded in 2007). No sampling was accomplished in 2003, 2004, or 2009. During the 19-year study period (16 sampling years) 155 hatchery individuals (13.0% of the 1192 stocked) were recaptured 1–5 times among 217 total recaptures. Of first-time recaptures, 63 (40.6%) were collected during 1993, the first year post-release (Table 2). Of the remainder, 35 (22.6%) were collected during 1994. Only 12 hatchery Gulf sturgeon were collected during 1995–1997, when USGS was using 10.2 cm bar mesh nets to census the subadult-adult population component, thereby missing most 3–5 year old juvenile hatchery fish. No hatchery Gulf sturgeon were obtained in sampling years 2008, 2010, and 2011 (Table 2); the most recent hatchery fish capture during the 1993–2011 study period occurred in 2007. However, sampling effort was low in those 3 years. No wild 1992 cohort Gulf sturgeon were obtained either in 2008 or 2010, and only one in 2011.

Hatchery fish recapture rates

The empirical or estimated TL ranges used to determine the total number of same-size wild Gulf sturgeon captured per sampling year for capture rate analyses are presented in Table 2. Resultant hatchery fish TL-at-age intervals by capture year are plotted in Fig. 2. Tagged hatchery Gulf sturgeon were recaptured in 13 of 16 sampling years, with recapture rates varying from 0.0 to 26.09% across the 16 years (Table 2).

Estimated hatchery fish population size

Estimated populations of surviving hatchery fish by recapture year are presented in Table 4. Variances are large and estimates are skewed by varying efforts between years. Estimates for 2003, 2004, and 2009 were set to null since no netting was conducted in those years. Effort in 2008, 2010, and 2011 was very limited, so model returns of zero for these years must be interpreted cautiously. The number of captures for analysis is lower than shown in Table 2 due to the elimination of within-year recaptures. Due to the nature of the fixed survival phi(.)p(t) model, the population estimates show less of a decline than the recapture percentages. Thus this model, by fixing survival throughout the study period, does not reflect the drop in hatchery fish recapture probabilities between 2000 and 2001. However, both time-varying phi(t) and biphasic (1992–2000; 2001–2011) age structured models had considerably less support under Akaike's Information Criterion coefficient (AICc) than the phi(.)p(t) model. Overall, what is apparent from both recaptures and estimated survivors is that the population of surviving hatchery fish had approached zero by 2008.

Estimated mortality rate

Null hypothesis H1 was rejected; the apparent mortality rate for hatchery Gulf sturgeon was more than twice that for wild spawned 1992 fish. The hatchery Gulf sturgeon apparent annual mortality rate determined from Program MARK 'phi' for the period of 1993–2011 was 26.7% (95% CI = 22.1–31.8%). The comparative rate determined for same-age, same-size wild Suwannee River Gulf sturgeon over the same period was 11.2% (95% CI = 4.2–26.8%) (Fig. 3, Table 3). Although the confidence intervals for the estimates overlap, this overlap is not highly informative. It is predominantly due to the restrictive selection criteria for inclusion of wild Gulf sturgeon individuals in formation of the pool of individuals available for analysis, resulting in comparatively small sample size (n = 224). The comparative mortality rate determined for the wild Gulf sturgeon population in the early through mid-1990s was 16% (Sulak and Clugston, 1999; Pine et al., 2001). This higher estimate for the mid-1990s (vs 11.2%, present study) is most probably attributable to added mortality from scientific netting through 1996, in an era where sampling mortality was not well controlled. For example, the 5.3% higher mid-1990s estimate vs the current estimate corresponds closely to the 5.0% net mortality documented in data from 3098 CCC and UF captures, 1984–1996 (Carr et al., 1996), and with the 5.7% net mortality

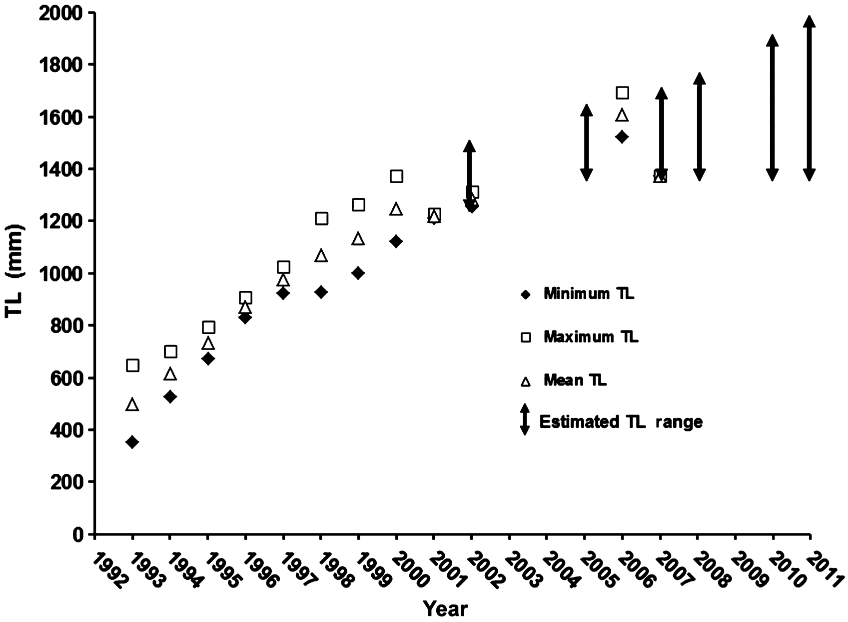

Fig. 2. TL range (minimum, maximum) and mean by year as observed for hatchery Gulf sturgeon captured (when N ≥ 3 for the given capture year), or as estimated from wild Gulf sturgeon TL-at-age data (when hatchery fish N < 3) for 1988-2011 net captures. No sampling was conducted in 2003, 2004, and 2009

Table 4
Program MARK population estimates by recapture year for surviving hatchery Gulf Sturgeons released into the Suwannee River, FL, in 1992, from phi(.)p(t) model

Year	Captures[a]	Pop estimate	95% confidence interval
1993	69	952	1224–744
1994	46	681	940–496
1995	5	467	1147–192
1996	6	413	10 028–168
1997	8	253	542–121
1998	39	214	355–136
1999	30	153	275–92
2000	5	102	279–39
2001	2	75	336–18
2002	2	30	149–7
2003			
2004			
2005	1	22	191–3
2006	3	16	76–5
2007	1	12	115–2
2008	0	0	
2009			
2010	0	0	
2011	0	0	

[a]Within-year recaptures excluded (vs Table 2).

present in the data from 6159 combined CCC, UF, and USFWS captures, 1988–1995 (USGS, unpubl. data).

Recaptures by release site

Over the course of the study hatchery fish from all ten 1992 release sites were recaptured (Table 1). There were zero capture mortalities. Comparative recapture rates (of fishes from all release sites) varied widely across the ten individual release sites, ranging from 1.52 to 52.53% (Table 1). Overall mean recapture rate across all release sites was 21.07%. Comparative 1992 wild Gulf sturgeon captures and recaptures by rkm sampling range are also displayed in Table 1.

Test of recapture rate among release sites

Null hypothesis H2 was rejected. That is, the χ^2 test revealed that hatchery fish recapture rates differed significantly among the ten release sites ($\chi^2 = 84.05$, critical upper value = 16.92, df = 9, $P < 0.001$). The two sites yielding the highest recapture rates as percent of all fish released were rkm 2 and rkm 8 (52.53% and 31.00%, respectively, together totaling 83 of 217 total recaptures) (Table 1) and are the two sites closest to the estuarine winter feeding grounds. Lowest recapture rates (1.52% and 6.09%, respectively, Table 1) were recorded for rkm 237 and the Santa Fe River site. Together these sites accounted for only 6.91% of total hatchery fish recaptures (Table 1).

Comparative growth rates

Comparative growth in terms of TL-at-age is displayed in Fig. 4 (through age 6000 days, i.e. the overall study period). A notable inflection in TL-at-age at age 3000 days for both hatchery and wild fish coincided with age-7 years. No corresponding inflection in growth was observed in terms of weight-at-age (through age 6000 days).

Test of comparative growth rates between 1992 hatchery and wild fish

Null hypothesis H3 was rejected for comparative growth rates expressed both as TL-at-age and as weight-at-age through age 3000 days. The slopes of comparative TL-at-age linear regressions for 1992 hatchery and 1992 year-class wild Gulf sturgeon differed significantly ($P < 0.0001$, ANCOVA, $F_{determined} = 454.47$, $F_{critical} = 3.87$, DF = 477) (Fig. 4). The

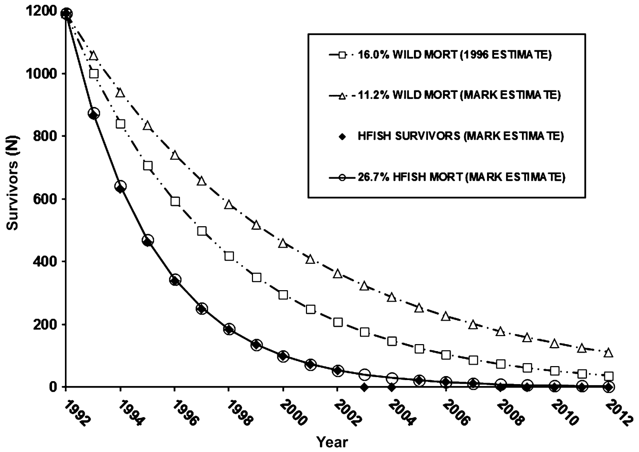

Fig. 3. Comparative hatchery Gulf sturgeon vs same-age wild Suwannee River Gulf sturgeon survivorship curves based on initial population sizes of 1192 fish in 1992. Hatchery fish apparent annual mortality of 26.7%, and wild fish apparent annual mortality of 11.2% are based on Program MARK mark-recapture 'phi' determined for the period 1993-2010. Comparative 16% wild fish annual mortality rate in mid-1990s from Sulak and Clugston (1999) and Pine et al. (2001)

slopes of comparative cube root transformed weight-at-age linear regressions for 1992 hatchery and 1992 year-class wild Gulf sturgeon through age 3000 days also differed significantly ($P < 0.0001$, ANCOVA, $F_{determined} = 17.28$, $F_{critical} = 3.87$, $DF = 468$) (Fig. 5). Thus, in terms of both TL-at-age and weight-at-age, hatchery fish grew at a significantly lower rate.

Test of relative recapture rates among years

Null hypothesis H4 was rejected. That is, the χ^2 test on annual hatchery fish relative recapture rates (Table 2) revealed that significant differences existed among the sampling years ($\chi^2 = 57.64$, critical upper value = 25.00, df = 15, $P < 0.001$). Annual relative recapture rate of hatchery fish (hatchery Gulf sturgeon captures as percent of total hatchery Gulf sturgeon recaptures plus same-size wild Gulf sturgeon captures) declined markedly from 1993 to 2011 (Table 2, Fig. 6). Moreover, relative recapture rate did not decline smoothly, as might have been predicted. Instead, a marked drop in relative recapture rate occurred between 2000 and 2001, corresponding to age-7 vs age-8 (Fig. 6). Based on graphical inspection, an *a posteriori* t-test comparing mean hatchery fish relative recapture rate over 1993–2000 (through age-8), vs that over 2001–2011 was undertaken. This revealed that the 1993–2000 mean recapture rate (17.41 ± 5.08% SD) was significantly higher than the mean 2001–2011 recapture rate (1.76 ± 1.81% SD) (t-statistic = 8.208, df = 14, $P < 0.001$).

Discussion

Recapture rate in relation to methodology

While sampling methods and relative effort varied substantially by year, influencing recapture totals, they were the same for both hatchery fish and 1992 cohort wild fish. Both were equally vulnerable to capture. Thus, as a proportion of captures of same-size, approximately same-age wild fish in a given year, hatchery fish recapture rate was effectively standardized.

Hatchery fish vs wild fish mortality

Hatchery fish appear to have encountered differentially higher mortality than same age wild Gulf sturgeon. Over the 19-year recapture period, estimated mortality rate (death + permanent emigration) for hatchery fish, based on Program MARK mark-recapture 'phi' determined for the period 1993–2010, was more than double (26.7%) that estimated for their 1992 cohort wild counterparts (11.2%). The USGS 2013 estimated mortality rate from all mark-recapture years data (1986–2013) using the CJS Open model was 11.7% ($N_{Total} = 5972$ captures, $N_{Recaptures} = 3061$) (USGS, unpubl. data).

Recapture rates by sampling year (Fig. 6) indicate that a notable decrease in hatchery fish survival coincided with the onset of full marine anadromy. One causal hypothesis would be potential failure of 220 days old hatchery-reared Gulf sturgeon to imprint on the Suwannee River as their natal river, resulting in permanent emigration simulating actual mortality. However, no Suwannee River 1992 hatchery fish (all PIT tagged) have been recaptured in any other Gulf sturgeon river (NOAA, unpubl. database from sturgeon researchers gulf-wide), including the annually well-sampled (1993–2011) Apalachicola River, the nearest neighboring natal sturgeon river.

Apparent imprinting failure among hatchery-released shortnose sturgeon, *Acipenser brevirostrum*, has been indicated for fish stocked in the Savannah River, some of which have unexpectedly been recaptured in other river systems (Smith and Collins, 1996; Quattro et al., 2002; Smith et al., 2002). However, in Suwannee River wild Gulf sturgeon, permanent emigration appears to be negligible. Emigration from the Suwannee River pool of tagged wild fish (>7000, 1988–2011) documented by USFWS tag recaptures in the nearest-neighbor sturgeon river (Apalachicola River) is <1% (six individuals) (USFWS, unpubl. data 1988–2011). Analyses of Gulf sturgeon mtDNA has shown that the species is differentiated into distinct regional or river-specific sub-populations (Stabile et al., 1996). Gene flow is extremely low and homing fidelity high, indicating very low permanent emigration. Microsatellite genotyping of 310 Suwannee River and 60 Apalachicola River Gulf sturgeon yields an estimated 1–4% rate of inter-river translocations (B. Kreiser, Univ. Southern Mississippi, pers. comm., 2012).

Hatchery fish recruitment to the adult population

The most recent estimate of Suwannee River wild Gulf sturgeon population size conducted in 2012–2013 was 8484 (95% CI = 6667–10 839) net-vulnerable (>1000 mm TL) subadults and adults (USGS, unpubl. data) The corresponding length frequency plot for the 2012–2013 sample showed that adults (>1350 mm TL) comprised ~50% of the population (USGS, unpubl.). Assuming adult population abundance in 2011 was

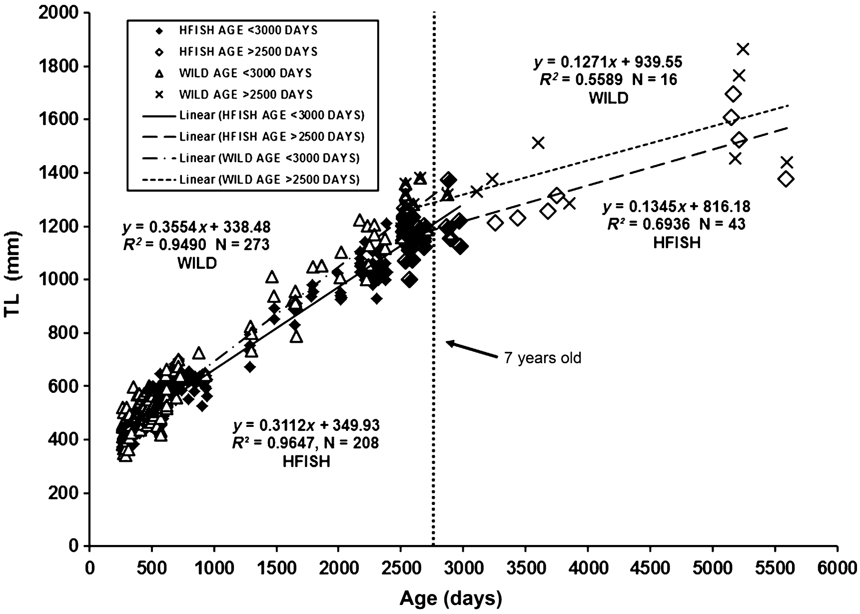

Fig. 4. TL-at-age (mm vs d) through age 6000 days (2011) for 1992 hatchery fish vs 1992 cohort wild fish. Growth rates to 3000 days were significantly different (ANCOVA, F test, F = 454.47, vs F_{crit} = 3.87. P < 0.0001)

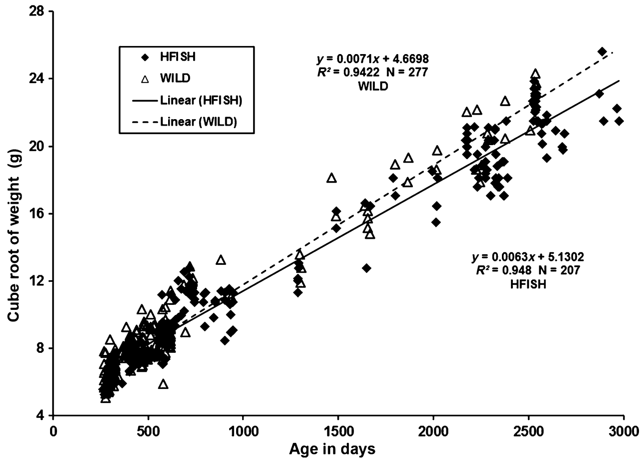

Fig. 5. Comparative cube root transformed weight-at-age (g vs d) through age 3000 days for 1992 hatchery fish vs 1992 cohort wild fish. Growth rates are significantly different (ANCOVA, F test, F = 17.28, vs F_{crit} = 3.87, P < 0.0001)

close to that in to 2012–2013, and assuming a 1 : 1 female: male sex ratio, females would have numbered approximately 4242 individuals in 2011.

Present results indicate that surviving hatchery females from the 1992 release would have made a negligible contribution to the overall Suwanee River Gulf sturgeon breeding population. Cumulative 26.7% apparent mortality through 2011 would have claimed 99.75% of the 1192 hatchery fish released in 1992. At onset of female Gulf sturgeon sexual maturity at age-12, there would be an estimated 28 surviving hatchery fish. At the expected 1 : 1 female:male sex ratio an estimated 14 potential female spawners would have entered the spawning population in 2004. An estimated three hatchery fish adults (1–2 females) would have survived through the end of the 19-year study period in 2011 (Fig. 3). Accordingly, hatchery females surviving to reproductive stage from the 1992 release would have comprised a negligible portion of the Suwannee River spawning population from the earliest predicted female maturity in 2004 (14 of 3450 = 0.41%) to the end of the study period in 2011 (2 of 4242 = 0.05%). This is reinforced by the results of Program MARK, which determine that zero hatchery Gulf sturgeon would have survived to 2011 (Table 4).

Survival rates from early life history through adult stages have not been determined for any sturgeon species in the wild. However, a comparative long-term hatchery fish survival rate is available for shortnose sturgeon in the Savannah River (Smith and Collins, 1996). In that experiment, 0.8% of 5074 tagged (PIT, anchor, and/or T-bar) hatchery fish (76–762 mm TL, age 2.5 months to 3 years old) released into the Savannah River, 1984–1992, were recaptured up to 3.9 years (mean = 1.4 years) post-release. In a subsequent 2000 update, Smith et al. (2002) reported that of 18 213 hatchery fish tagged (among 97 483 fingerlings released), only 52 were recaptured, yielding <0.3% survival at year-10 post-release (compared to 3.28% survival at year-10 post-release in the present hatchery Gulf sturgeon release experiment). Comparative survival to adult size for the tens of millions of hatchery fry (released primarily at age 30–50 days) of Russian sturgeon (*Acipenser gueldenstaedtii*), beluga (*Huso huso*), and stellate sturgeon (*A. stellatus*), stocked annually since the mid-1950s in the Volga-Caspian system has been reported as 0.1–1.0% (Khodorevskaya et al., 1995, 1997; Levin, 1995; Luk'yanenko et al., 1999).

Importance of release site to hatchery fish survival

Recapture site did not correlate closely with initial release site. Thus, although 198 Gulf sturgeon had been released at rkm 2 in December 1992, 30 of 40 recaptures at this site during the first 6 months of 1993 were fish from upstream release sites.

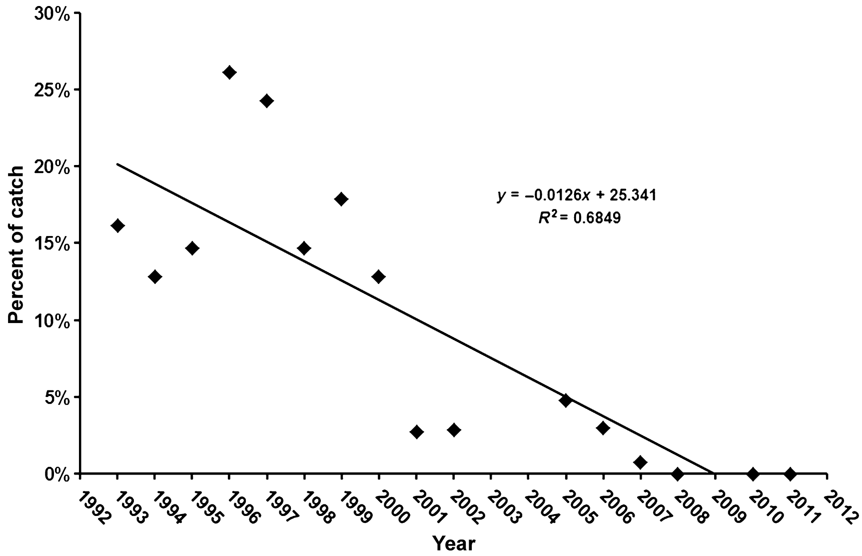

Fig. 6. Suwannee River hatchery Gulf sturgeon recapture rates per sampling year (post-1992 release), as percent of total catch of hatchery Gulf sturgeon plus same-size (TL) wild Gulf sturgeon for a given sampling year (Table 1)

However, the release site appears to have been important to survival success. The rkm 2 and rkm 8 release sites yielding the highest recapture rates were those nearest the river mouth winter feeding grounds. These sites offered the advantage of a very short post-release downstream migration to the feeding grounds. Conversely, the two sites (rkm 237 and the Santa Fe River site, 155 rkm upstream) yielding the lowest hatchery fish recapture rates (1.38% and 5.53%, respectively) represent the two most atypical fingerling habitats. Hatchery fish released at rkm 237 faced low water temperatures at the outset (10.7°C vs 13.0–14.7°C at release sites below rkm 215) and the longest downstream migration to the estuary. Hatchery fish released at the Santa Fe River site faced unusual and unfavorable habitat conditions for fingerlings. To migrate downstream, they first had to navigate underground caverns for 5 rkm (Hellier, 1966) between the river sink and rise (Fig. 1), then traverse 41 rkm of shallow, rocky-bottom, clear-water habitat, atypical Gulf sturgeon habitat. The USGS 25-year database documents only three wild Gulf sturgeon captures in the Santa Fe River (USGS, unpubl. data). In two comparative U.S. East Coast sturgeon hatchery release studies (Smith and Collins, 1996; Secor et al., 2000) release site also appeared important to survival success.

Hatchery fish growth and fitness

Growth rates in terms of length (TL-at-age) and weight (cube root transformed weight-at-length) were significantly lower for hatchery fish through age 3000 days (Figs 4 and 5) than for wild fish. This suggests lower fitness compared to that of their wild 1992 cohort counterparts. Hatchery sturgeon displayed the same inflection (reduction) in length increment per year between age-7 and age-8 (Fig. 4) as did wild fish, suggesting a common life history juncture in length gain. However, there was no corresponding reduction in rate of weight increase for either hatchery or wild fish.

Mortality effects on potential population enhancement

The decline in recaptures of hatchery Gulf sturgeon over the course of this study (Table 2), despite increasing capture availability each year in our gill nets, corresponds with expectations. Even for wild fish, with an apparent annual mortality rate of 11.2–16.0% (Sulak and Clugston, 1999; Pine et al., 2001; present study), the predicted cumulative mortality over 19 years would be 88–96%. The Suwannee River population mortality rate range is very closely matched by empirical or derived natural mortality rates (10–16%) reported for protected or closely-managed populations of wild populations of North American sturgeon species, including lake sturgeon, *Acipenser fulvescens* (Threader and Brousseau, 1986; Bruch, 1999), white sturgeon, *Acipenser transmontanus* (Miller, 1972; Kohlhorst, 1980), and shortnose sturgeon (Dadswell, 1979). Thus, the comparatively much higher mortality rate for hatchery Gulf sturgeon in the present study may be informative in considering the potential effectiveness of any hatchery supplementation plan for this species. The 12–16 year time span until first sexual maturity for female Gulf sturgeon means that cumulative mortality will be the mathematically inescapable nemesis (Boreman, 1997) of any population restoration attempts based on stocking of cultured fingerlings. Accordingly, from the results of the present experiment, very high numbers of Gulf sturgeon fingerlings would have to be released to achieve any substantial increase in the size of the effective breeding population. At the observed 26.7% hatchery fish mortality rate, 265 000 age-220 days Gulf sturgeon fingerlings would result in approximately 250 females surviving to age-12, the potential first year of their sexual maturity.

Hatchery stocking as a population recovery strategy for the Gulf sturgeon: management - implications from the release experiment

The Gulf sturgeon recovery plan (USFWS, GSMFC, NMFS 1995) stated that: "…stocking should be secondary to other recovery efforts that identify essential habitats and emphasize habitat restoration." Population supplementation would be undertaken only if determined necessary to aid restoration. Exercise of this hatchery supplementation contingency was advocated by Chapman et al. (1997), who suggested that the Suwannee River population was the only viable reproductive population for the species but that it was not increasing. However, both 1997 conclusions have proven erroneous. Subsequent mark-recapture studies have shown that at least four (Choctawhatchee, Yellow, Apalachicola, Escambia rivers) of the seven known Gulf sturgeon natal rivers contain populations of several hundred to several thousand individuals (Fox et al., 2000; Berg et al., 2007; U.S. Fish and Wildlife Service, 2008; Pine and Martell, 2009) composed of multiple size classes (i.e. multiple year-classes), evidence of regular reproduction and recruitment. Furthermore, successful natural reproduction has also been demonstrated by collection of wild sturgeon eggs in not only the Suwannee River (Marchant and Shutters, 1996; Sulak and Clugston, 1998, 1999; Parkyn et al., 2007), but also the Choctawhatchee (Fox et al., 2000), Yellow (Kreiser et al., 2008), Escambia (Craft et al., 2001), Apalachicola (Scollan and Parauka, 2008; Flowers et al., 2009), and Pascagoula (Slack et al., 1999) rivers. In the Suwannee River following the 1984 harvest ban, Sulak and Clugston (1999) estimated that the Gulf sturgeon population had more than doubled from 2000 to 3000 net-vulnerable (>1000 mm TL) fish to over 7500 by the mid-1990s.

Natural population recovery in the Suwannee and in other Gulf sturgeon rivers following harvest prohibition suggests that supplementation via release of hatchery-reared fish does not appear to be necessary in rivers where trenchant habitat limitations or human impacts do not exist. Allowing natural recovery to take place in the Suwannee River has avoided the potential of disease transfer, habitat swamping, and genetic risks incumbent with releases of cultured anadromous fishes (Hindar et al., 1991; Waples, 1991; Fleming, 1994; Busack and Currens, 1995), including the Gulf sturgeon (Tringali and Bert, 1998). It has also avoided the simulated mortality effects (reduction of lifetime eggs per recruit) (Boreman, 1997) upon the wild population of removing wild adult females from the river to serve as broodstock. Boreman's (1997) sturgeon mortality curves demonstrate that protecting adult females in a long-lived, late-maturing fish species (in which juveniles are subject to cumulative high mortality prior to achieving sexual maturity) is more important to population maintenance and restoration than adding age-0 recruits to the population. The age-structured Suwannee River Gulf sturgeon population model of Pine et al. (2001) reinforces the mathematical impacts upon wild populations advanced by the Boreman (1997) and Tringali and Bert (1998) models. Pine et al. (2001) concurred with Boreman (1997), concluding that for the Suwannee population: "....adult survival was more important to population growth than recruitment rates." By logical inference, this may be interpreted as a critique of Gulf sturgeon supplemental stocking, which is aimed at increasing recruitment rates. Accordingly, it is a critique as well of the fundamental first step in launching hatchery culture of Gulf sturgeon, i.e. the removal of adult females from the wild population to enable hatchery culture aimed at enhancing recruitment. Pine et al. (2001) stated: "... removal of mature females for spawning and recovery efforts could reduce recruitment of wild fish." Thus, the initial step toward launching a hatchery supplementation program can have a direct and immediate negative conservation impact upon an imperiled sturgeon species.

Conclusions

The 19-year follow-up of the Suwannee River Gulf sturgeon hatchery release experiment undertaken in 1992 demonstrated that hatchery fish performed poorly compared to the 1992 wild cohort. Annual recapture rate of hatchery Gulf sturgeon declined markedly from 1993 to 2011, with a dramatic drop between 2000 and 2001, corresponding to the age-7 to age-8 juncture. This coincides with the age of transition to full marine feeding, which may represent a critical period in Gulf sturgeon survival. Additionally, hatchery fish post-release growth rates in length and weight were significantly lower than for their 1992 year-class wild counterparts through age 3000 days, suggesting comparatively lower fitness. Overall, the mark-recapture annual hatchery fish mortality rate estimated for the 19-year period (1993–2011) was more than twice as high (26.7%) than for the same 1992 wild sturgeon cohort (11.2%).

Release site proved to be important to hatchery fish survival, with the two lowermost release sites (rkm 2 and rkm 8) yielding the highest rates of recapture riverwide, suggesting that release sites closest to winter estuarine feeding grounds performed best. The two most atypical release sites, the furthest upriver site (rkm 237) and a site above the sink in the Santa Fe River tributary (rkm 155), yielded the lowest recaptures riverwide.

The present study suggests that hatchery supplementation as a Gulf sturgeon conservation measure does not appear to be an effective option. However, survival of Gulf sturgeon hatchery fish might be enhanced by streamside rearing (allowing for natal river imprinting), utilization of a genetically-sound mating design producing multiple families from unique male-female spawning pairs (potentially improving survival fitness), and release of fingerlings only at sites close to the rivermouth (reducing downriver migration distance, energetic cost, and predation risk). Rearing fingerlings to age 7–8 months for release in early winter appears to be a sound option to coordinate release timing with the onset of first estuarine feeding, and to minimize predation risks in the wild during age 1–7 months.

Acknowledgements

Experimental culture and release of Gulf sturgeon involved substantial collaboration with USFWS (F. Parauka), the CCC (S. Carr, F. Tatman), and UF (F. Chapman). The Lower Suwannee National Wildlife Refuge (K. Litzenberger) and Welaka National Fish Hatchery (A. Brown) contributed logistics and expertise. Additional logistic support came from the National Marine Fisheries Service (Southeast Fisheries Center, Miami); USFWS (Ecological Services, Panama City, FL); and Florida Wildlife Research Institute. USFWS/USGS recapture data were supplemented by additional data from CCC (S. Carr) and UF (D. Colle). USFWS/USGS assisting personnel included W. Harden, G. Hill, D. Houkom, J. Noble, L. Parker, S. Traxler, and G. Yeargin. Our sincere thanks go to the large number of volunteers who assisted in the field work. The authors express their thanks for valuable critique of early drafts by D. Colle, F. Parauka, D. Secor, and T. Smith; final reviews by M. Price, B. Gillett, and U. Nash, and the constructive critique of the anonymous reviewers.

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